New stem giraffoid ruminants from the early and middle Miocene of Namibia

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ABSTRACT

At the early and middle Miocene localities of the Sperrgebiet, Namibia, new material of climacoceratid ruminants have been collected recently. From Elisabethfeld we describe new material belonging to *Propalaeoryx austroafricanus* Stromer, 1926, together with a new genus and species of climacoceratid *Sperrgebietomeryx wardi* n. gen., n. sp., a species without frontal appendages close to *Propalaeoryx* and to primitive early Miocene European ruminants such as *Andegameryx*. From the locality of Arrisdrift, we define another new genus and species of climacoceratid with frontal appendages, *Orangemeryx hendey* n. gen., n. sp., characterized by its complex tined frontal apophyses. Comparison of the dentition and postcranial skeleton of this genus and those of *Sperrgebietomeryx* suggests a close phylogenetic relationships between them.

KEY WORDS
Ruminantia,
Giraffoidea,
Climacoceratidae,
Miocene,
Namibia.

RÉSUMÉ

Nouveaux ruminants giraffoïdes du Miocène ancien et moyen de Namibie.
Dans les localités du Miocène inférieur et moyen de la Sperrgebiet en Namibie, de nouveaux restes de ruminants Climacoceratidae ont été récemment récoltés. Un nouveau matériel provenant d'Elisabethfeld appartenant à *Propalaeoryx austroafricanus* Stromer, 1926 est décrit, ainsi qu'un nouveau genre et une nouvelle espèce de Climacoceratidae, *Sperrgebietomeryx wardi* n. gen., n. sp., espèce ne possédant pas d'appendices frontaux, proche de *Propalaeoryx* et des ruminants primitifs du Miocène inférieur européen, comme *Andegameryx*. À Arrisdrift, nous décrivons un autre genre et une autre espèce de Climacoceratidae avec des appendices frontaux, *Orangemeryx bendeyi*, qui se caractérise par ses apophyses frontales complexes. Les comparaisons entre la denrition et le squelette postcrânien de ce genre et de ceux de *Sperrgebietomeryx* suggèrent une proche parenté phylogénétique entre les deux.

MOTS CLÉS
Ruminantia,
Giraffoidea,
Climacoceratidae,
Miocène,
Namibie.

INTRODUCTION

This is the second report on the ruminants of the early and middle Miocene of Namibia collected by the Namibia Palaeontology Expedition. The first paper dealt with the small bovid *Namibiomeryx senuti* Morales *et al.*, 1995. In this article we describe the giraffoids from the same region.

Two new genera of giraffoids recovered from the sites of Elisabethfeld and Arrisdrift in southern Namibia (Fig. 1) reveal a great deal about the origins of this superfamily of ruminants. The new climacoceratid giraffoids lack frontal apophyses, and occur in the early Miocene deposits at Elisabethfeld and other sites in the northern part of the Sperrgebiet. *Sperrgebietomeryx* is closely related to primitive late Oligocene European ruminants such as *Andegameryx* Ginsburg *et al.*, 1994, and lies close to the root of the group which subsequently developed apophyses, the Giraffoidea. *Sperrgebietomeryx* occurs in the same strata as another sperrgebietomerycine, the genus *Propalaeoryx* Stromer, 1926.

Basal middle Miocene deposits at Arrisdrift have yielded abundant remains of a new genus of climacoceratid, *Orangemeryx*, a climacoceratine
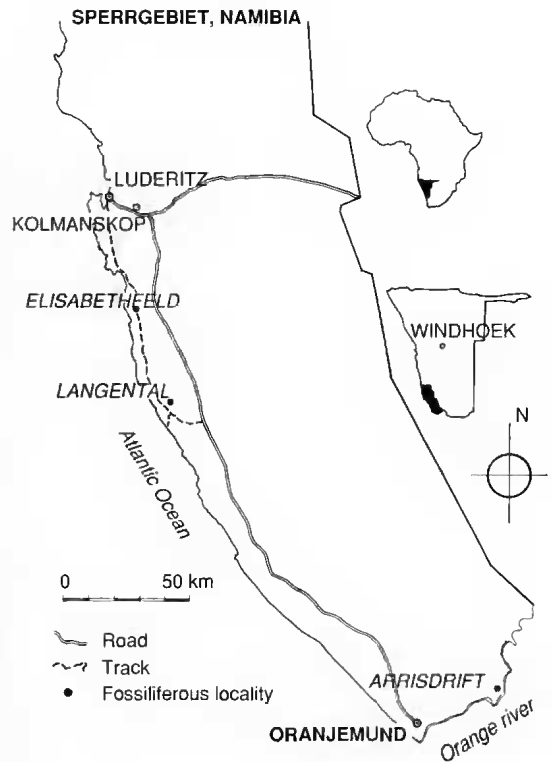

FIG. 1. — Geographical location of Arrisdrift (early middle Miocene) and Langental and Elisabethfeld (early Miocene) in the Sperrgebiet, southern Namibia.

with tined apophyses. Examination of the skull and postcranial skeleton of this genus and those of *Sperrgebietomeryx* suggests that the Arrisdrift species may well be the descendant of the Elisabethfeld one.

The transition from primitive pecorans to climacoceratids with apophyses thus appears to have occurred in Africa subsequent to colonization of this continent by pecorans from Eurasia.

GEOLOGICAL SETTING

ELISABETHFELD

The early Miocene site of Elisabethfeld (Stromer 1926) occupies one of a series of pre-Miocene valleys which used to drain into the Atlantic Ocean from the region of the present-day Namib Sand Sea. As a result of a worldwide rise in sea-level during the early Miocene the transient sediments in the valleys stopped moving, and further sedimentation occurred in the drowned valleys. At Elisabethfeld, fine-grained red limey silts accumulated in a plain that lay between the Grillental and one of its southern tributaries which had cut through Proterozoic rocks. These red silts, which are often overprinted with pedogenic features, were incised and then buried by green silts, sands and conglomerates. These fluviatile beds are overlain by a fine-grained palaeodune sequence (Greenman 1966, 1970; Corbett 1989). Unconformably overlying the early Miocene sediments is a two metre thick travertine which has invaded the upper portion of the aeolianite. Fragments of this travertine have been incorporated into a younger set of aeolianites which crop out extensively in the area, often filling palaeo-valleys cut into the early Miocene sediments.

At the base of one of the green, pebbly-sand channel infillings cropping out as a low cliff and immediately overlying the basal red limey silts, the partial skeleton of a ruminant was observed by Drs J. Ward and I. Corbett in June, 1993. The specimen was photographed and left *in situ* for later excavation. In August, 1993, Drs M. Pickford and B. Senut visited the site with J. Ward and excavated the skeleton. It was evident that at least 1 cm of sediment had been

removed, principally by sand-blasting, since the photographs had been taken two months previously. A mandible with the cheekteeth in place in June had eroded so that only the ventral margin of the jaw was left in August.

The associated fauna indicates that the Elisabethfeld skeleton is of early Miocene age. The site correlates broadly with the localities of Songhor and Koru, Kenya, and is thus interpreted to be about 20-21 Ma old (Faunal Set 1 of Pickford 1981).

ARRISDRIFT

The site of Arrisdrift occurs in a lateral channel of the Proto-Orange located about 1 km east of the present-day channel of the river. Fossiliferous sediments lie at an altitude of about 41 m above mean sea-level, infilling a low channel carved into the Gariep Group of Late Proterozoic age. The channel is filled with a complex cut-and-fill sequence of sediments ranging in grain size from conglomerates to clays, the latter representing clay-drapes deposited during periods when the Arrisdrift channel was cut off from the main river. During periods of high water, the channel would be active, so that numerous scour and fill episodes occurred, and can be seen in superposition in the excavation.

During periods of low water level, the channel was effectively isolated from the main stream and would have been a quiet pool of water. This channel lay close to sea-level, as indicated by the presence of serpulid worm tubes in abundance, even to the extent of forming serpulid reefs. Today these invertebrates live in brackish water in estuarine settings. There can be little doubt that at the beginning of the Middle Miocene, some 17.5-17 Ma ago, sea-level was some 41 m above present day levels.

The site of Arrisdrift, like the earlier ones in the northern Sperrgebiet, owes its formation to the world-wide rise in sea-level that occurred at the end of the early Miocene, which caused the back-ponding of sediments within the Proto-Orange valley. The difference in ages of the fossil sites in the northern and southern Sperrgebiet indicate that the rise in sea-level was relatively slow, the highest stand being reached some 2-3 Ma later than the onset of rising sea-levels.
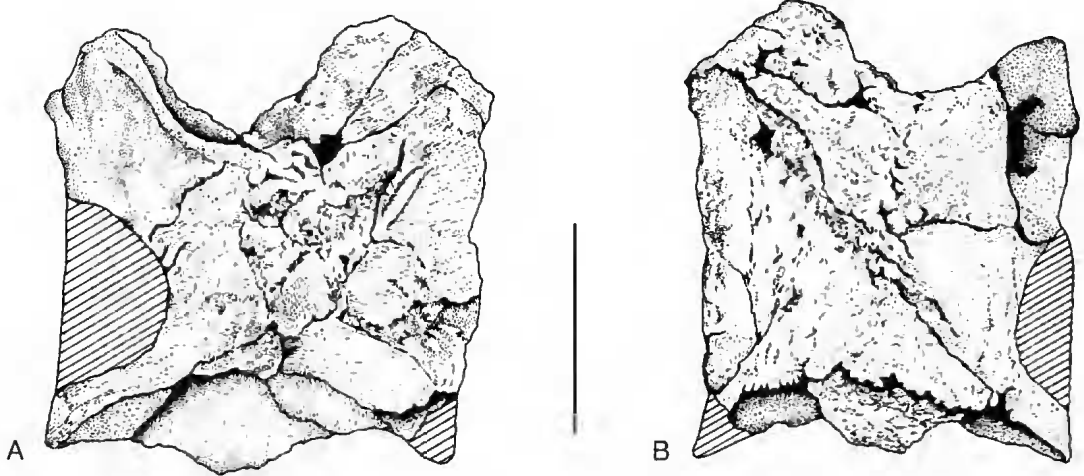
Fig. 2. — Atlas of *Sperrgebietomeryx wardi* n. gen., n. sp. (EF 37'92); **A**, dorsal view; **B**, ventral view. Scale bar: 20 mm.

This scenario is confirmed by the discovery of early Miocene mammals at Auchas, another Proto-Orange deposit, in sediments 32-37 m above present-day mean sea-level, or some 10 m lower than the deposits at Arrisdrift.

By the time that sea-levels dropped again later in the middle Miocene, the Proto-Orange river had abandoned some of its meander loops and was following a less sinuous course towards the coast. When incision occurred following lowering of base-levels, the early and middle Miocene sediments deposited in many of the abandoned loops were left high and dry.

The fauna associated with *Orangemeryx* is early middle Miocene in age, correlating closely with European zone MN4 (De Bruijn *et al.* 1992) and with the sites of Buluk and Maboko in Kenya, assigned to Faunal Set PIII (Pickford 1981). It is probably about 17.5-17 Ma (Pickford 1994).

SYSTEMATIC PALEONTOLOGY

Suborder RUMINANTIA Scopoli, 1777
Superfamily GIRAFFOIDEA Simpson, 1931

Family CLIMACOCERATIDAE Hamilton, 1978
(= CLIMACOCERIDAE Hamilton, 1978)

DIAGNOSIS. — Ruminants of medium to large size characterised by the tendency – in relation to other ruminants of the same age – for elongation of the neck (including the atlas) and limbs. Distal epiphysis of the metatarsal with open gully. Dentition with a clear hypsodont tendency. Palaeomeryx fold in lower molars moderate or suppressed, hypoconid isolated and lobe of m3 simple.

SPERRGEBIETOMERYCINAE n. subfam.

TYPE GENUS. — *Sperrgebietomeryx* n. gen.

DIAGNOSIS. — Climacoceratidae without cranial protuberances. Cranium with wide frontals, sagittal crest and nuchals strongly defined. Dentition moderately hypsodont. Premolar series elongate. Lower molars with strong stylids and moderate paleomeryx fold. Upper molars with very strong styles and late union of the internal lobes with the outer wall.

Sperrgebietomeryx n. gen.

TYPE SPECIES. — *Sperrgebietomeryx wardi* n. sp.

DIAGNOSIS. — The same as for the type species.

Sperrgebietomeryx wardi n. sp.

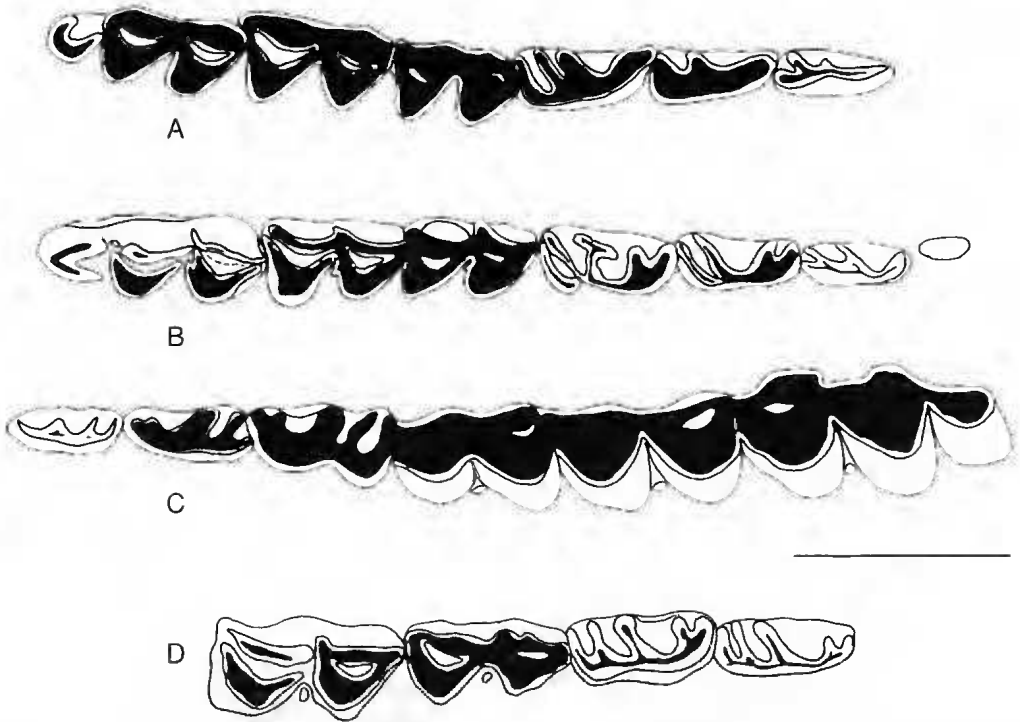cf. *Strogulognathus sansaniensis* Filhol (Stromer 1926).

FIG. 3. — Occlusal view of the lower dentition of fossil ruminants from the Sperrgebiet, southern Namibia; **A**, right m3-p2 of *Sperrgebietomeryx wardi* n. gen., n. sp. (EF 37'93), from Elisabethfeld; **B**, right m3-p2 and alveolus of p1, *Propalaeoryx austroafricanus* Stromer (EF 3'93), from Elisabethfeld; **C**, left m3-p2 of *Orangemeryx hendeyi* (AD 1521), from Arrisdrift; **D**, left m2-p3 of *Orangemeryx hendeyi* n. gen., n. sp. (AD 654'94), from Arrisdrift. Scale bar: 20 mm.

HOLOTYPE. — EF 37'93, skull, mandible and associated atlas, with parts of the vertebral column and hind limbs (Figs 2, 3A, 4, 5, 10F-H), housed in the Museum of the Geological Survey of Namibia, Windhoek.

TYPE LOCALITY AND AGE. — Elisabethfeld, Namibia. Early Miocene.

ETYMOLOGY. — *Sperrgebiet*, German name for the "forbidden territory" on account of this name applied to the Diamond Area of southern Namibia; *meryx*, Greek for deer. The species name honours geologist Dr John Ward who found the holotype.

DIAGNOSIS. — Medium-sized giraffoids, premolar series long and gracile. Lower p4 with simple metaconid, directed posteriorly, anterior wing without bifurcation. P2 and p2 nearly the same size as P3 and p3.

DIFFERENTIAL DIAGNOSIS. — *Sperrgebietomeryx* differs from *Propalaeoryx austroafricanus* by its smaller size, by the more primitive morphology of the p4 and P4, and the loss of p1. It differs from *Walangania africana*

(Whitworth 1958) by its larger size, the more gracile premolars and the more primitive construction of the p4 and P4. It differs from *Prolibytherium* Arambourg, 1961, Giraffidae and Climacoceratinae by the absence of cranial protuberances which are present in the latter three groups.

DESCRIPTION
The skull (Figs 3-4) is well preserved, although eroded on the anterior part of the left side, and slightly crushed dorsoventrally. In ventral view the skull presents a clearly primitive morphology, comparable to that of *Dremotherium* (Sigogneau 1968). The auditory region is of primitive type, with the styloid process located between the mastoid process and the tympanic bulla, the latter being moderately inflated, while the external auditory meatus is prominent and almost circular. The basioccipital is relatively wide, with strong posterior and anterior tubercles for muscle insertions. The width of the insertion zone for the
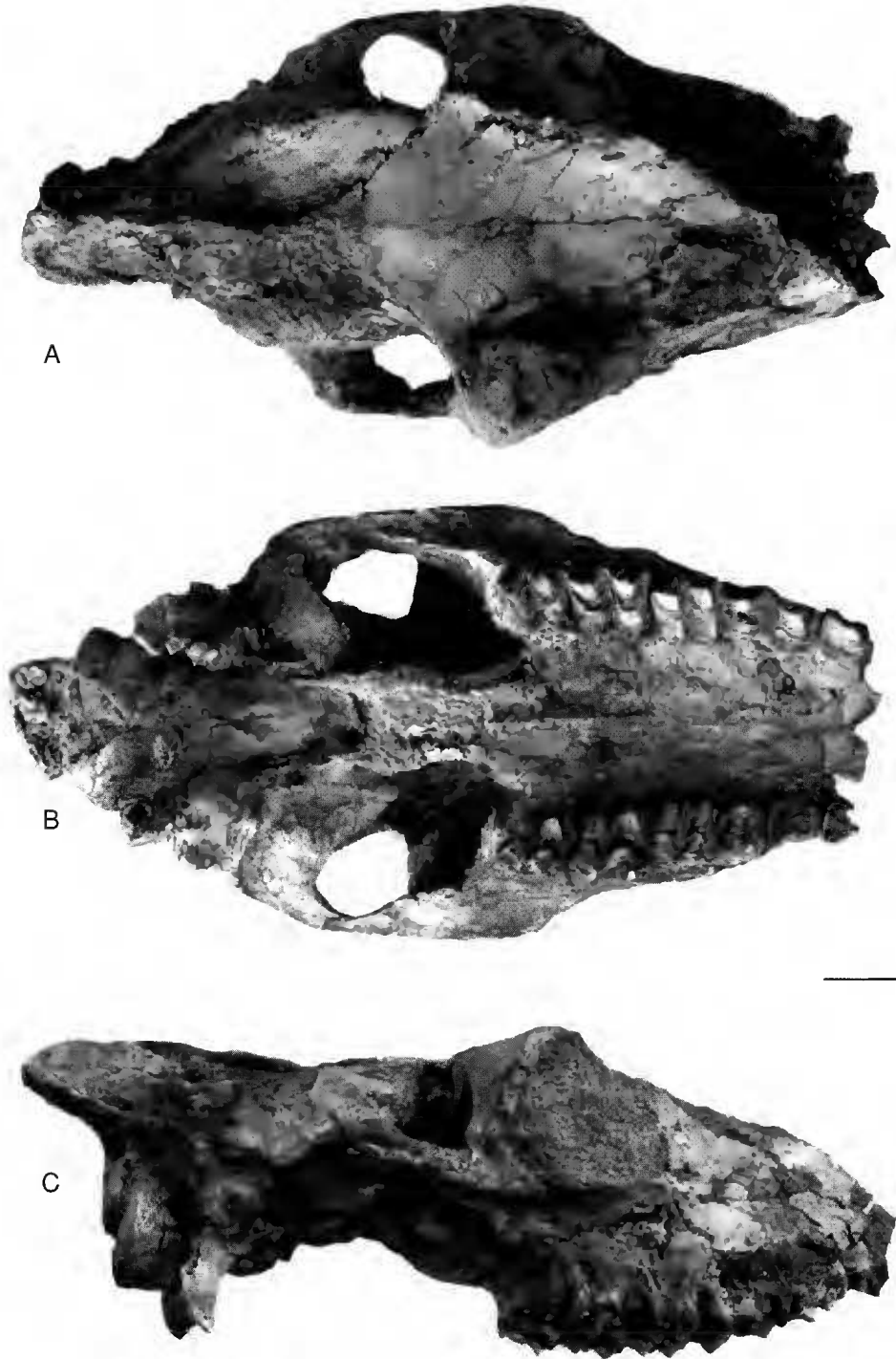
Fig. 4 — *Sperrgebietomeryx wardi*, n. gen., n. sp., holotype skull, Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **A**, dorsal view; **B**, ventral view; **C**, right lateral view. Scale bar: 20 mm.

TABLE 1. — Measurements (length, width, in mm) of the upper dentition of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld (EF 37'93), *Propalaeoryx austroafricanus* from Elisabethfeld (EF 4'93) and *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift.

| | S. wardi | | P. austroafricanus | | | O. hendeyi | | |
	r EF 37'93 l		EF 4'93	EF200'93	EF201'93	AD273	AD283'94	AD334'95
LMM-PP	68.0	–						
LMM	39.5	38.2	41.5			63.0		
LPP	31.0	–	–					
LM3	13.5	13.0	14.0			21.6		
WM3	12.8	12.3	–			18.2		
LM2	13.6	13.5	15.1			21.4		
WM2	15.5	15.2	–			21.9		
LM1	13.5	12.2	13.0			21.0		
WM1	13.0	12.2	–			20.0		
LP4	10.0	9.5	10.5	11.4		13.1		
WP4	10.0	10.5	–	10.3		15.9		
LP3	10.0	10.7					11.5	
WP3	9.5	9.2					13.2	
LP2	10.4	–			12.5			14.1
LP2	8.9	–			–			11.8

masseter muscles is remarkable, and reveals their strength. In dorsal view, the width of the frontals, the strength and height of the sagittal crest and of the nuchal crest are all notable features of the skull. The zygomatic process of the frontal is very prominent. The frontals are relatively wide, although they appear wider on account of the dorsoventral compression that affects the skull. There is no lacrimal fossa, and there may have been an ethmoidal fenestra although the preservation of this part does not allow of certainty in this matter. The external occipital protuberance is very strong and projects posteriorly. The supraoccipital has a well-marked crest.

Upper dentition (Table 1, Fig. 4B)
Molars with strong parastyles and mesostyles; in the M3 the metastyle is also strong. The internal

TABLE 2. — Measurements (length, width, in mm) of the lower dentition of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld (EF 37'93), cf. *Strogulognathus* (Stromer 1926); *Propalaeoryx austroafricanus* from Elisabethfeld (EF 3'93) and Langental (1926-507, holotype), cf. *Strogulognathus sansaniensis* from Langental (Stromer 1926) and *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift.

| | S. wardi EF 37'93 | cf.Strogulog. l | P. austroafricanus | | N | O. hendeyi OR | M |
			EF 3'93	1926-507			
LMM-PP	75.0		82.0	90.6	9	95.0-109.0	100.6
LMM	44.0		48.2	52.8	12	58.0-65.5	62.1
LPP	32.0		34.9	37.0	13	34.6-45.5	38.6
Lm3	18.5	18.0	21.5	21.2	14	24.2-29.0'	26.7
Wm3	8.0	8.0	8.5	9.0	13	9.5-11.5	10.6
Lm2	13.6	13.0	13.0	15.5	17	17.0-21.5	20.2
Wm2	8.9	9.0	7.9	9.4	17	10.2-13.0	11.9
Lm1	12.5		12.5	14.8	16	15.2-20.5	16.7
Wm1	7.9		7.0	8.8	16	9.3-12.0	10.5
Lp4	12.2		12.5	13.0	18	12.5-15.5	14.5
Wp4	5.7		7.7	6.5	18	8.0-10.0	8.9
Lp3	10.9		12.0	12.4	13	11.3-15.1	14.1
Wp3	5.5		6.5	–	13	6.0-8.2	7.3
Lp2	9.5		10.2	10.5	8	9.0-12.5	9.9
Wp2	4.1		5.0	4.3	8	4.0-5.7	4.8
Lp1			5.0	6.0			
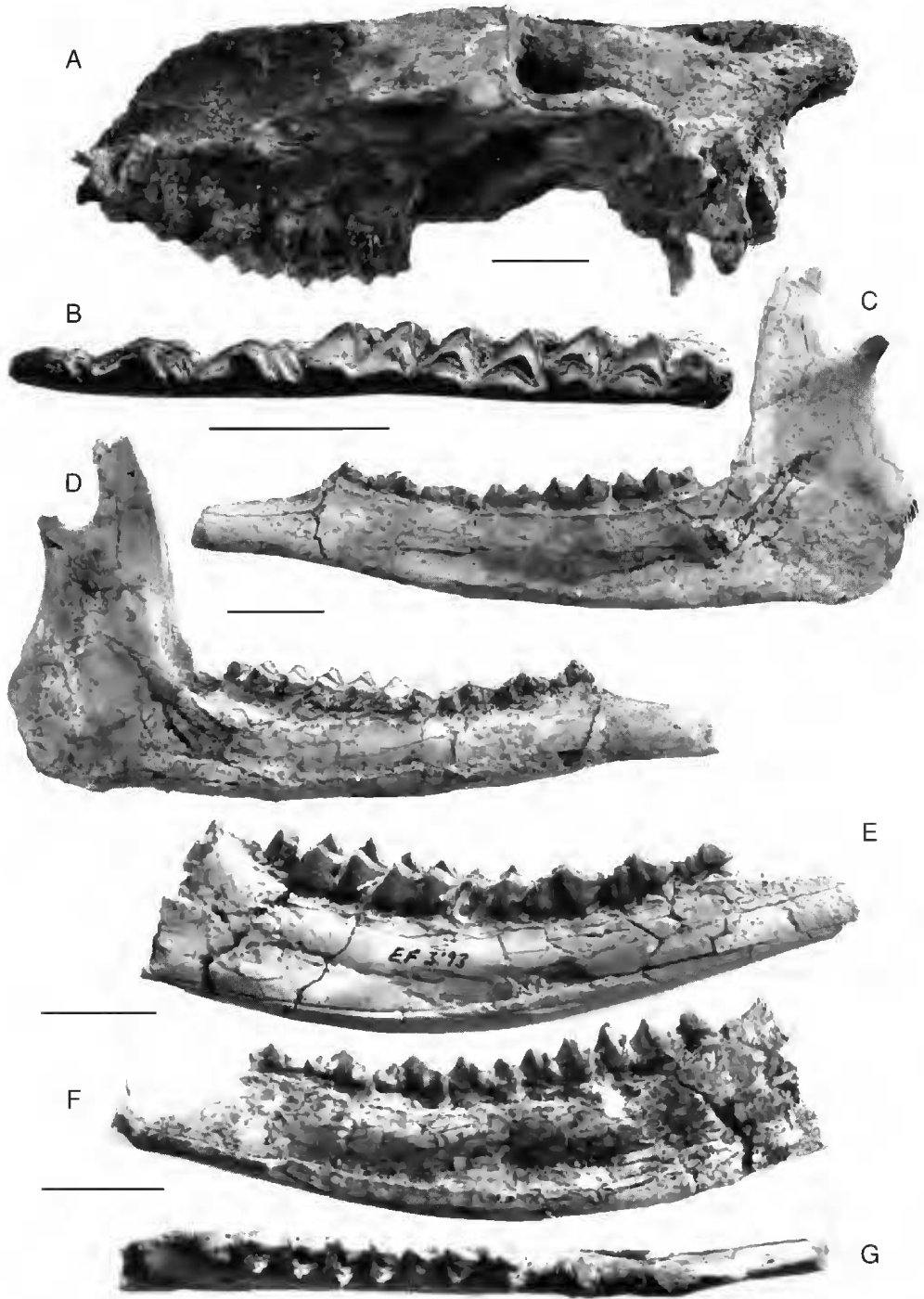
FIG. 5. — **A-D**, *Sperrgebietomeryx wardi* n. gen., n. sp., Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **A**, holotype skull in left lateral view; **B-D**, right mandible; **B**, occlusal view of cheek dentition; **C**, lingual view; **D**, buccal view; **E-G**, *Propalaeoryx austroafricanus*, Stromer, Elisabethfeld red silts, northern Sperrgebiet, Namibia, early Miocene; right mandible; **E**, buccal view; **F**, lingual view; **G**, occlusal view. Scale bars: 20 mm.

lobes fuse late with each other, the interlobular column is small. M2 is larger than the other two molars, which are approximately the same size. The premolars are long, including the P4, which possesses a strong anterior style with a cingulum round the protocone. P3 and P2 also possess a strong anterior style and a well-defined anterior lobe [close morphologically to the premolars of Boselaphini (Bovidae)].

Lower dentition (Table 2, Fig. 5B-D)
The stage of wear prevents much being observed, especially in the molars. The third lobe of m3 is relatively small. The premolars are long and gracile. The close morphological similarity between the premolars is notable, especially between p3 and p4. Both premolars have simple metaconids directed posteriorly and the anterior wing without bifurcation, while the external incision is moderate.

DISCUSSION
The existence of two ruminant species in the early Miocene of the northern part of the Sperrgebiet was noted by Stromer (1926) on the basis of fossils from Langental and Elisabethfeld assigned by him to cf. *Strogulognathus sansaniensis* Filhol, 1870 and *Propalaeoryx austroafricanus* Stromer, 1926, respectively. The dentitions assigned to *Strogulognathus* were slightly smaller than those assigned to *Propalaeoryx austroafricanus*, but were otherwise similar to them, which is why they have subsequently been pooled with those of *P. austroafricanus* (Hamilton & Van Couvering 1976).

Genus *Propalaeoryx* Stromer, 1926

TYPE SPECIES. — *Propalaeoryx austroafricanus* Stromer, 1926.

HOLOTYPE. — 1926-507, mandible.

TYPE LOCALITY. — Elisabethfeld, Namibia.

NEW COLLECTIONS. — Elisabethfeld, Namibia: EF 3'93, right mandible (Table 2, Fig. 5E-G); EF 4'94, fragment of right maxilla with damaged P4-M3; EF 200'93 right P4; EF 2001'93 left P2 (Table 1).

DESCRIPTION
The mandible has lost the ascending ramus and the symphyseal portion. The horizontal ramus is robust and preserves the alveolus for p1 which is uniradiculate. The lower molars possess a moderate paleomeryx fold, most marked in the m1. The metastylid is strong and isolated. The posterior wing of the hypoconid is well separated from the entoconid. The basal pillar is of moderate size. The hypoconulid of the m3 is simple and of moderate size. The p4 presents a bifurcate anterior wing and complex metaconid positioned in front of the protoconid and forming an incipient internal wall. There is a deep vertical incision in the posterior part of the external wall. The p3 is much simpler. It also has a bifurcate anterior wing, but the metaconid is a simple crest directed backwards. The p2 is smaller than p3 with a simple anterior wing. The dimensions (in mm) of the specimen are as follows: molar series 48.2; premolar series (without the p1) 34.9; m3 21.5×8.5; m2 13×7.9; m1 12.5×7; p4 12.5×7.7; p3 12×6.5; p2 10.2×5; p1 (alveolus) 5×2. The maxilla fragment is badly abraded so that the internal lobes of the four teeth P4-M3 have been partly destroyed, so that only the external length of the teeth can be measured, as follows (in mm) : M3 14; M2 15.1; M1 13; P4 10.5. In the three molars the parastyle and mesostyle are well-developed and externally well-defined. In the M3 there is, in addition, a strong metastyle which is also well defined externally and which is united by a basal cingulum to the other styles. The P4 is elongated with strong parastyle and metastyle.
The isolated P4 (11.4×10.3 mm) has an external wall similar to that in the specimen described above. The protocone is surrounded by a relatively strong cingulum.
The isolated P2 (length 12.5 mm) is missing its protocone. The parastyle is large and globular. The paracone is well marked externally and is joined to the parastyle by a smooth cingulum which continues to the posterior margin.

DISCUSSION
The Elisabethfeld *Propalaeoryx* mandible differs from that of *Sperrgebietomeryx* by its larger size, the presence of a well-developed p1 and premolars which are more robust and complex. The p4s are particularly different, those of

Propalaeoryx Stromer, 1926, possessing a bifurcate anterior wing, a strong metaconid which forms an incipient lingual wall, and a deep external incision. In all these characters this specimen is close to the holotype mandible of *Propalaeoryx*

austroafricanus, although the latter is slightly larger and has a simpler metaconid in its p4. The new jaw from Elisabethfeld has hypsodont molars and, as in the holotype, the palaeomeryx fold is weak, being strongest in the m1.

TABLE 3. — Measurements (in mm) of the postcranial skeleton of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld and *Propalaeoryx austroafricanus* from Elisabethfeld and Langental (Stromer 1926). Abbreviations: **APD**, antero-posterior diameter; **TD**, transversal diameter; **c.c.**, corpus calcanei; **t.c.**, tuber calcanei; **m.**, maleolus; **s.**, sustentaculum.

		S. wardi		Stromer, 1926	*P. austroafricanus*
RADIUS	EF 21'94	EF 23'94	EF 24'94	8	EF 41'94
Length	214.0				
Proximal APD	15.9			16.0	17.7
Proximal TD	27.9			28.0	31.5
Distal APD			19.4		
Distal TD		25.6	25.1		

	S. wardi	*P. austroafricanus*
HUMERUS	EF 36'94	EF 22'93
Distal APD	28.0	30.0
Distal TD	28.6	34.1

	S. wardi	Stromer, 1926		
SCAPHOID	EF 23'94	10α	10β	10γ
Anterior Height	13.1	13.0	12.5	14.8
APD	17.2	18.5	19.0	20.5

	S. wardi	Stromer, 1926
SEMILUNAR	EF 23'94	9
Anterior Height	12.4	12.0
Proximal APD	16.3	
Proximal TD	13.5	14.5

	S. wardi	Stromer, 1926
FEMUR	EF 37'93	15
Proximal TD	50.0	52.0
Head APD	22.1	20.0
Head TD	28.1	27.0

	S. wardi		
METACARPAL	EF 35'93	EF 23'94	EF 24'94
Length	207.2		205.0
Proximal APD	17.3		17.8
Proximal TD	21.4	22.1	
Distal TD	23.8		

	S. wardi	Stromer, 1926	
TALUS	EF 37'93	18a	18b-β
Lateral Length	31.4	31.0	35.5
Medial Length	29.9		
Lateral APD	18.3		
Distal TD	20.2	19.0	21.2

	S. wardi	*P. austroafricanus*
CALCANEUM	EF 37'93	EF 36'93
Length	70.9	
c.c. Length	49.0	50.3
t.c. APD	18.4	20.2
t.c. TD	17.8	18.4
c.c. APD	18.9	18.3
c.c. TD	8.6	9.9
m. APD	25.9	
s. TD		21.3

	S. wardi	Stromer,1926	
TIBIA	EF 37'93	16α	16β
Length	257.0		
Proximal APD	46.0		
Midshaft APD	17.8		
Midshaft TD	20.7		
Distal APD		23.5	24.0
Distal TD	29.0	31.0	30.0

	S.wardi		P.austroafricanus	Stromer, 1926
I PHALANX	EF 24'94	EF 27'94	EF 28'94	13α
Length	34.7	39.8	43.5	42.0
Proximal APD	13.7	15.2	16.2	
Proximal TD	12.2	14.3	13.9	13.0
Distal APD	9.4	9.5	9.9	
Distal TD	10.1	12.1	11.5	

	S.wardi	Stromer, 1926
II PHALANX	EF 24'94	13β
Length	20.4	21.5-25.0
Proximal APD	12.0	
Proximal TD	10.2	
Distal APD	10.7	
Distal TD	7.9	7.5-9.0

	S.wardi	
III PHALANX	EF 24'94	EF 34'94
Plantar Length		22.3
Dorsocaudal D	17.4	
Dorsoplantar D		13.7

The upper dentition of *Propalaeoryx austroafricanus* was hitherto unknown, and the attribution of the new Elisabethfeld specimen to this species is based on its discovery locus, its size (larger than *Sperrgebietomeryx*) and its more robust premolars.

POSTCRANIAL SKELETON OF *Sperrgebietomeryx* AND *Propalaeoryx*
Vertebral column

Articulated with the holotype skull of *Sperrgebietomeryx wardi* there was the atlas (Fig. 2) and three cervical vertebrae (the axis, V3 and V4). The atlas is notable for its elongation, being almost as long as it is wide, and in this respect resembles the atlas of several antelopes such as *Gazella dama* Pallas, 1766. The margins of the wings are virtually parallel and straight. The axis and the other vertebrae are poorly preserved, only V3 being complete and revealing that it too was elongated.

Limb bones

Elisabethfeld has yielded some thirty ruminant limb bones, in addition to the partial skeleton found with the holotype skull and mandible of *Sperrgebietomeryx wardi*. Many of the specimens have been sand-blasted and some are broken, so it is often difficult to assign them taxonomically. Because of the uncertainty in identifying to which species the bones belong we describe the specimens together, but suspect that the larger specimens belong to *Propalaeoryx austroafricanus* Stromer, 1926, while the others probably represent *S. wardi* (Table 3).

Specimens EF 22'93, a distal humerus (Fig. 10E), EF 41'94, a proximal radio-ulna, EF 36'93, the body of a calcaneum, and EF 28'94, a first phalanx, are assigned provisionally to *P. austroafricanus*.

The following specimens are assigned to *S. wardi*: EF 36'94 and EF 22'94, distal humeral epiphyses; EF 21'94, a complete radius; EF 23'94, articulated juvenile radial epiphysis, carpus and proximal end of metacarpal; EF 24'94, articulated radius, metacarpal and phalanges; EF 35'93, complete metacarpal; EF 37'93, proximal half of a femur, tibia, talus, calcaneum found with the holotype skull, mandible and atlas; EF 27'94, first phalanx; EF 34'94, third phalanx.

Humerus

S. wardi has the radial fossa limited by a tuberosity which reaches the lateral epicondyle, and is very large because the capitulum has a moderate vertical development and proximally does not ascend greatly, while distally it stays at the same level as the trochlear groove. The humerus of *P. austroafricanus* is similar but it is slightly wider, has a medial condyle which is less well-developed proximodistally, and has very strong relief in the medial epicondyle
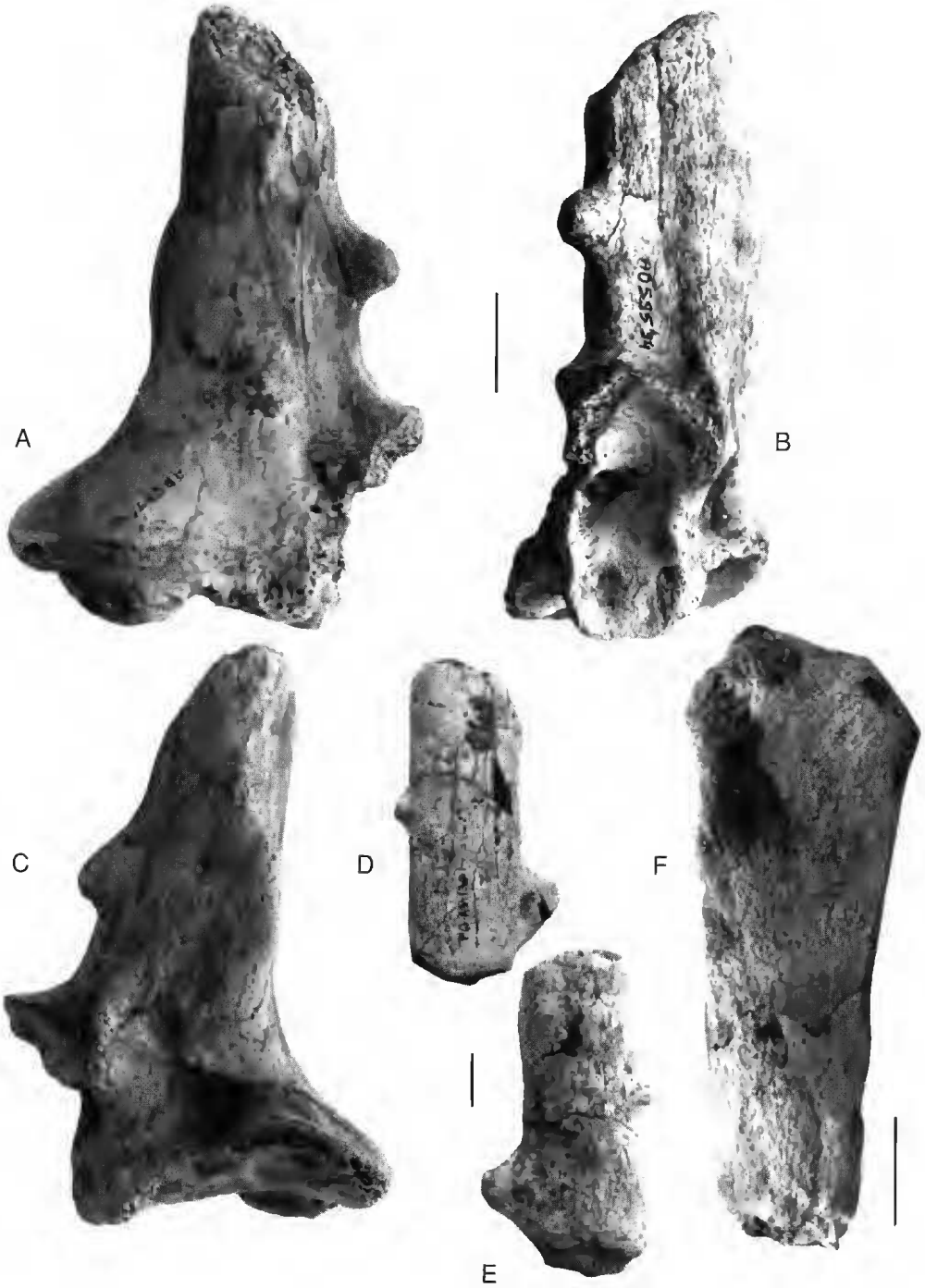
FIG. 6. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A-C**, holotype frontal with base of left apophysis (AD 595'94); **A**, medial view; **B**, frontal view; **C**, lateral view; **D**, **E**, lower part of apophysis lateral views (AD 130); **F**, mid-part of apophysis with base of bifurcation towards top of frame (AD 131). Scale bars: 20 mm.

Radius

The proximal epiphysis is the same in the two species, but in *P. austroafricanus* it is slightly bigger and the lateral tuberosity is stronger. The diaphysis in EF 21'94 (Fig. 10G) is gracile, and the articular facets of the distal epiphysis in all the specimens have the typical morphology of early Miocene ruminants; that of the pyramidal is small and horizontal, whereas that for the scaphoid is larger and more elevated than that of the semilunar and there is a platform for the ulna contact.

Carpus

The material is articulated making it difficult to observe all the morphological details (Fig. 10F). The semilunar is subquadrangular and the distal lateral facet is much wider than the medial one, also its morphology and measurements are identical to those of cf. *Strogulognathus sansaniensis* Filhol, 1870, cited by Stromer (1926, pl. 40, fig. 4).

Metacarpal

This bone is long and gracile (Fig. 10H), the diaphysis having a flat posterior surface, and the proximal extremity being narrow with respect to the antero-posterior diameter. The facet for the magnotrapezoid is very large compared to that for the unciform. The distal pulleys have well-developed keels posteriorly.

Femur

The proximal half is preserved but both trochanters are broken. On the posterior surface, below the lesser trochanter, there is a roughened triangular area delimited by two crests which continue parallel to the length of the diaphysis as in the extant giraffid species *Okapia johnstoni* (Sclater 1901).

Tibia

This bone is also long, gracile and straight. The tibial crest is long, reaching to mid-shaft of the diaphysis. On the posterior surface next to the popliteal line there is another line parallel to it and somewhat shorter, also as in *Okapia*. The medial distal groove is wide and shallow. In distal view the anterior and posterior margins of the epiphysis are markedly concave and the wall which separates the trochlear facets is short anteroposteriorly.

Astragalus

Corresponding to the morphology of the distal tibia, the depression between the two condyles of the proximal end is deep and is also asymmetrical. In the medial condyle there is a strong posterior process, and on the anterior surface on both sides of the fossa there are well-developed stop facets. On the distal end, the lateral condyle is more extensive than the medial one.

Calcaneum

The calcaneum of *Sperrgebietomeryx wardi* has a symmetrical tuber with a wide but short and deep posterior fossa. Its body is straight, the distal lateral groove is smooth and the distal facet for the astragalus is oblique. In the calcaneum of *P. austroafricanus* the tuber is asymmetric and more strongly developed, both transversely and antero-posteriorly. The rugose postero-medial area is also more developed.

Metatarsal

The only specimen in the collection is a distal juvenile fragment (EF 25'94) that shows an open anterior groove. Its attribution to *Sperrgebietomeryx wardi* is based on its size.

Subfamily CLIMACOCERATINAE Hamilton, 1978

DIAGNOSIS. — Climacoceratidae with frontal protuberances of apophyseal nature (Bubenik 1990). Dentition hypsodont. Premolar row shortened. Lower molars without palaeomeryx fold. Upper molars with external fusion of the lingual and buccal lobes.

Orangemeryx n. gen.

TYPE SPECIES. — *Orangemeryx hendeyi* n. sp.

DIAGNOSIS. — As for the type species.

Orangemeryx hendeyi n. sp.

Climacoceras sp. – Hendey 1978.

HOLOTYPE. — AD 595'94, left frontal fragment with

FiG. 7. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, apophyseal point (AD 1798); **B**, apophyseal point (AD 1177); **C-F**, apophysis with trifurcate tip (AD 594'94); **C-E**, various views; **F**, dorsal view; **G, H**, bifurcate apophyseal tip, lateral views (AD 649 + 763). Scale bars: 20 mm.

apophysis, housed at the Geological Survey of Namibia, Windhoek (Fig. 6A-C).

ETYMOLOGY, — For the Orange River which is the border between Namibia and South Africa and *meryx* the Greek word for deer. The species is dedicated to palaeontologist Dr Q. B. Hendey.

DIAGNOSIS. — Climacoceratinae with elongated slightly compressed truncate conical supraorbital apophyses, ornamented at the base with rounded tubercles with bifurcated or trifurcated upper termination (two or three points).

DIFFERENTIAL DIAGNOSIS. — *Orangemeryx* differs markedly from the other two genera of climacoceratines by the morphology of its apophyses, which are short with a wide base which diminishes towards the apex, giving the apophysis an elongated, slightly compressed truncated conical aspect, different from the cylindrical form that occurs in *Nyanzameryx* Thomas, 1984 and *Climacoceras* MacInnes, 1936.

DESCRIPTION

Holotype: The frontal bone is very thick and strongly vascularised but not enough to be called pneumatised. The supraorbital foramen is well-defined and externally continues to the apophysis following a smooth canal. The postcornual fossa is deep and continues posteriorly as a wide but not very deep, well-demarcated groove. The apophysis is in the form of an elongated compressed cone, with the base wide and diminishing in section towards the apex, while the base is compressed transversally (antero-posterior diameter = 44.5 mm, transversal diameter = 29.0 mm), whereas towards the apex the section is almost circular. There is a smooth anterior keel, accompanied by a small protuberance, the posterior margin is rounded with a weaker but more extensive protuberance. The apex is broken, so that it is possible to observe that the wall of the apophysis is thick and the central part vascularised (Fig. 8E).

Other specimens such as AD 130 (Fig. 6D-E), AD 250, AD 483, AD 596'94 (Fig. 8A-E) and AD 132 (Fig. 8F-G), are similar to the holotype,

even though there is a certain amount of variability in the shape and size of the protuberances of the apophyses. At the base of the apophysis in AD 596'94 (Fig. 6A-E), there are shallow sinuous canals indicating the courses followed by blood vessels, which suggest that the apophyses were covered in skin. AD 131 (Fig. 6F) is the apical and medial part of an apophysis which possesses a lateral protuberance similar to those mentioned above. This specimen indicates that the apophysis bifurcates towards the apex, also evidenced by the surface ornamentation in the form of a Y. Other specimens indicate a more complex apex than this fossil, one of which AD 648+763 (Fig. 7G), illustrated by Hendey (1978) shows a tip with two different sized points, while another AD 594'94 (Fig. 7C-F) is trifurcate with three approximately similar sized points. Fragments of apophyses such as AD 129 (figured by Hendey 1978) or AD 1798 (Fig. 7A), AD 1177 (Fig. 7B), AD 658'94 and AD 659'94, are probably best interpreted as points at the apex of the apophysis.

A specimen of skull (AD 652'94, Fig. 9B-D) comprises the frontal with the base of the apophysis and part of the parietal back to the union of the temporal lines, where they begin to form the sagittal crest. There is a strong, abrupt change in slope between the parietal and the frontal, while between and anterior to the apophyses there is a deep, rounded depression. In the base of the right apophysis there is a deep, strong postcornual fossa similar to that observed in the holotype, which continues distally as a canal to connect with the temporal line. The temporal lines are well-marked, swelling towards the base of the apophyses, and posteriorly they unite to form a visible thickening, which in the broken surface has a subtriangular section. There was probably a strong development of the nuchal crest. The frontals are very thick and the bone is well vascularised, in particular the large supraorbital foramen which expands into the roof of the orbit. The bases of the apophyses are not pneumatized, and in the right one the long wide voluminous base can be observed, while in the left one, which is more broken, the subtriangular transversal section can be seen to be similar to that in AD 596'94. This cranial fragment is
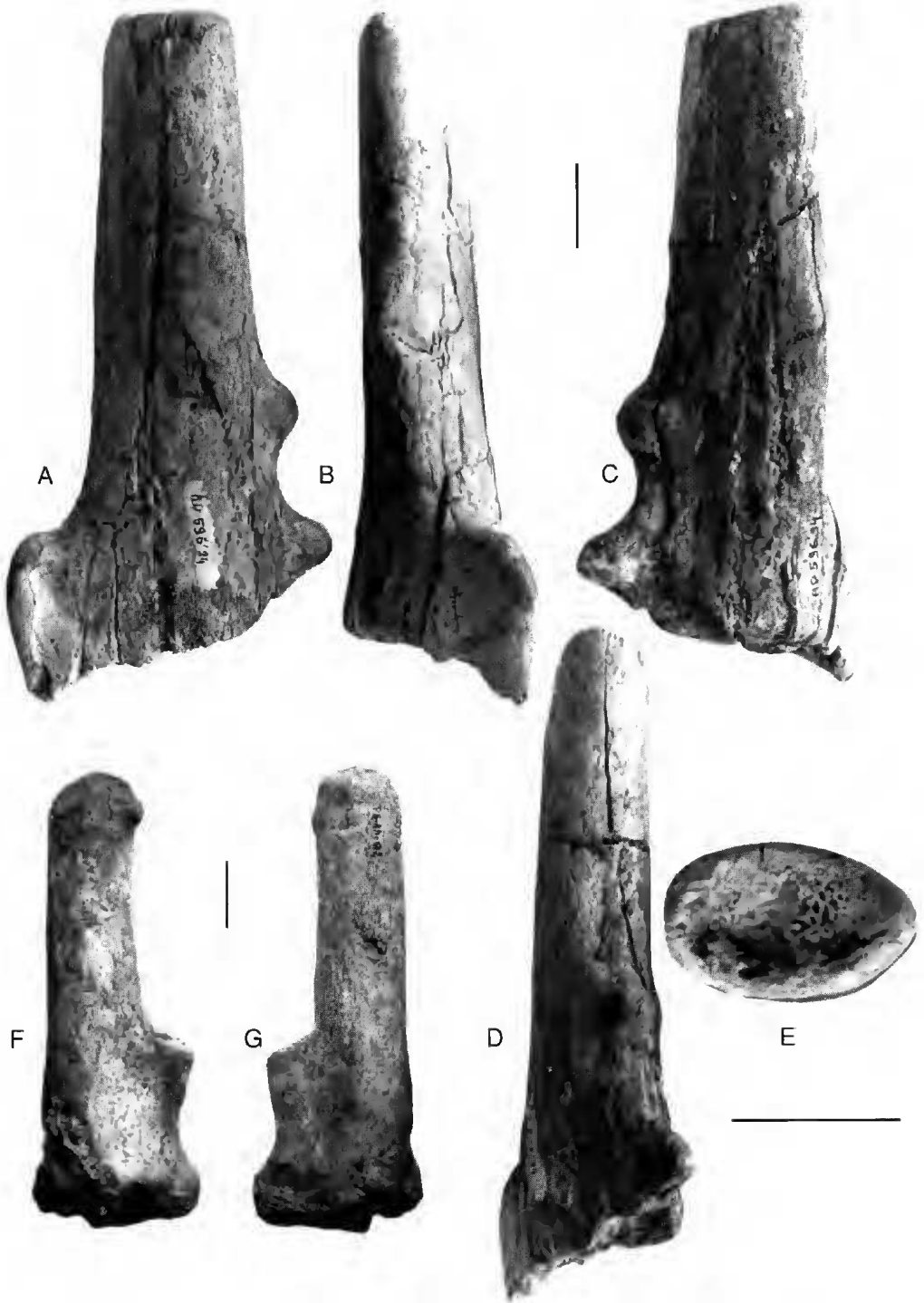
Fig. 8. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A-E**, left apophysis (AD 596'94); **A**, medial view; **B**, posterior view; **C**, lateral view; **D**, anterior view; **E**, transversal cross section; **F, G**, base of apophysis, two views (AD 132). Scale bars: 20 mm.
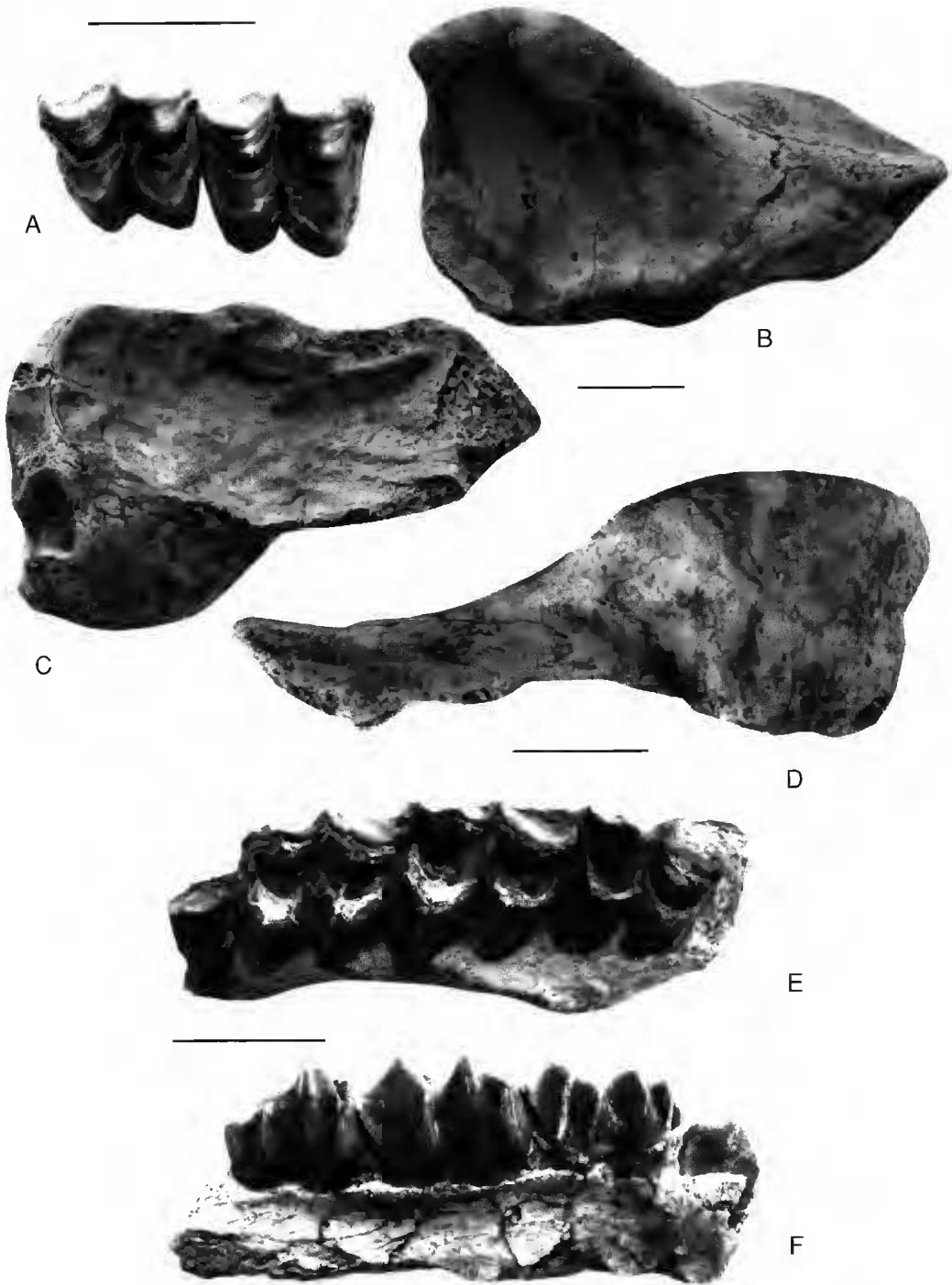
FIG. 9. — *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, left D4-M1 in occlusal view (AD 624); **B-D**, cranial fragment (AD 652'94); **B**, dorsal view; **C**, ventral view; **D**, right lateral view; **E**, **F**, left P4-M3 (AD-273); **E**, occlusal view; **F**, buccal view. Scale bars: 20 mm.

Fig. 10. — **A-D**, *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A, B**, axis (AD 1549); cervical vertebra V3 (AD 1447); **A**, lateral view; **B**, dorsal view; **C**, left radius, anterior view (AD 00'95); **D**, left metatarsal, anterior view (AD 5'93); **E**, *Propalaeoryx austroafricanus*, Stromer, Elisabethfeld red silts, northern Sperrgebiet, Namibia, early Miocene, left distal humerus, anterior view (EF 22'93); **F-H**, *Sperrgebietomeryx wardi* n. gen., n. sp., Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **F**, left juvenile distal radius, carpus, and proximal metacarpal (in anatomical connection), anterior view (EF 23'94); **G**, right radius, anterior view (EF 21'94); **H**, left metacarpal, posterior view (EF 35'93). Scale bars: 20 mm.

useful in providing evidence as to the correct orientation of the apophyses in *Orangemeryx*, especially the holotype AD 595'94, in which it was inclined slightly laterally and forwards.

Dentition

The cheek teeth are relatively hypsodont, being similar in many respects to the dentition of other climacoceratids. Lower molars (Table 2, Fig. 3C) possess strong metastylids which project laterally. The protoconid and hypoconid are flattened. The hypoconid and protoconid are separated, only uniting when wear is advanced. The hypoconulid of m3 is simple and unicuspidate. The premolars are short. The p4 is variable, always with the anterior wing bifurcate and a strong labial groove, the metaconid varies from being isolated to forming a wall which unites with the metastylid. Incisiform teeth are well represented in the collection, none of which are bilobed. Upper molars (Table 1, Fig. 9A, E, F) have internal lobes separated from each other. The styles are strong, particularly the parastyle and merastyle. The entostyle is weak. Upper premolars are short and wide.

Vertebral column

Numerous vertebrae of *Orangemeryx hendeyi* are preserved, some of them in articulation. All in all they possess morphological features typical of modern ruminants. Among the cervical vertebrae there is an axis (AD 1549, Fig. 10A-B) which is relatively complete. It is notably elongated and the spinous process is distinctly high and well-developed, which suggests the existence of strong musculature related to movements of the head. A further well-preserved cervical vertebra (AD 1447, Fig. 10A. B), like the previous specimen, is elongated.

Limb bones

The sample of limb bones assigned to *Orangemeryx hendeyi* is very comprehensive, bones of this species being the most common mammal remains at the site (over 220 specimens). In the sample are complete examples of most limb elements, but some of them have been deformed by compaction and several have been damaged by gypsum crystal growth (Table 4, Fig. 10C, D). The morphology of the limbs is quite generalized,

except for their elongation, indicating that *O. hendeyi* was not greatly specialized, retaining much of the aspect of what we consider to be the basal giraffoid condition. Many of the postcranial elements of these ruminants possess a rather constant morphological pattern, whereas others present major variability and appear to be more closely implicated in the processes of adaptation and evolution, even though it is difficult to determine their evolutionary significance. The existence of great variability in the bone size is also noticeable, which should probably be interpreted as a dimorphic pattern. The aim of this section is not to provide a detailed study of each postcranial element, but to provide remarks on the salient features of the limb skeleton of *O. hendeyi*.

Humerus

In the proximal epiphysis (Fig. 11A), the greater and lesser tuberosities are low and there is no intermediate tubercle equivalent to the condition in more modern giraffes. The distal epiphysis is comparable to that of *Sperrgebietomeryx wardi* described above, but the radial fossa is more reduced due to the great proximo-distal development of the capitulum and the medial condyle of the trochlea, a condition which also differentiates it from *Climacoceras gentryi* and *Palaeotragus primaevus*, the humeri of which possess a more "giraffid"-like morphology with the medial condyle low proximally.

Radioulna

The proximal epiphysis of the radius accords with the morphology of the distal humerus, and this bone thus differs in the same way from its counterpart in *P. primaevus*; the lateral facet is higher and the medial one more inclined in *O. hendeyi*. The distal radial epiphysis is similar to that described in *S. wardi*, the diaphysis is quite straight and is antero-posteriorly compressed. The ulna (Fig. 11B-C) is not fused to the radius. Its tuber olecrani possesses high lateral and medial crests, between which is a deep valley, similar to a specimen of *Climacoceras gentryi* Hamilton, 1978, from Ngorora, Kenya.
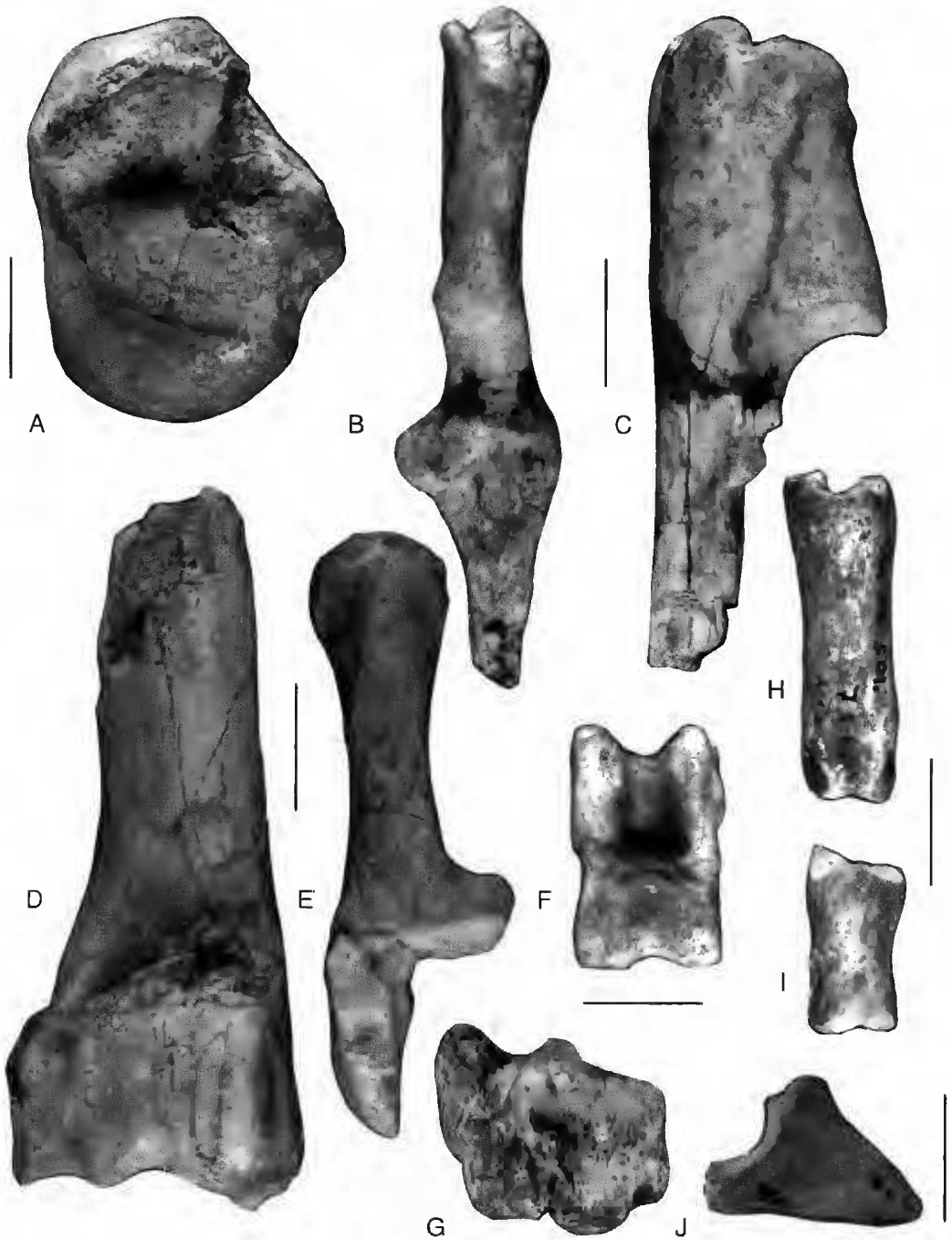
Carpus

The scaphoid retains the distal posterior facet

FIG. 11. — *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, left proximal humerus, proximal view (AD 3380); **B-C**, right proximal ulna (AD 00'95); **B**, anterior view; **C**, lateral view; **D**,right distal humerus, anterior view (AD 1915) ; **E**, right calcaneum, anterior view (AD 747); **F**, right talus, anterior view (AD 613'94); **G**, right navicular cuboid, posterior view (AD 317'95); **H**, I Phalanx, anterior view (AD 501); **I**, II Phalanx, anterior view (AD 469); **J**, III Phalanx, lateral view (AD 896). Scale bars: 20 mm.

TABLE 4. — Measurements (in mm) of the postcranial skeleton of *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift. Abbreviations: **APD**, antero-posterior diameter; **TD**, transversal diameter; **c.c.**, corpus calcanei; **t.c.**, tuber calcanei; **m.**, maleolus; **s.**, sustentaculum.

	N	OR	M
Humerus			
Length	1		209.5
Proximal APD	3	64.0-71.2	68.0
Proximal TD	1		54.8
Distal APD	6	41.8-48.6	45.2
Distal TD	6	44.6-51.8	47.5
Radius			
Length	9	254.0-287.0	268.0
Proximal APD	10	20.4-26.8	23.8
Proximal TD	10	37.0-46.8	42.1
Midshaft APD	9	14.1-22.3	18.1
Midshaft TD	9	23.0-33.4	28.2
Distal APD	12	23.7-32.9	28.6
Distal TD	13	34.0-46.5	39.5
Ulna			
Olecranon Length	4	49.7-61.0	54.6
Tuber o. APD	4	30.1-37.4	33.6
Tuber o. TD	1		15.2
Pro. anc. APD	6	32.6-45.6	39.0
Proc. anc. TD	9	11.3-14.4	12.7
Scaphoid			
Anterior Height	6	17.4-21.6	19.5
APD	6	24.3-28.5	26.3
Anterior TD	5	12.3-14.6	13.8
Semilunar			
Maximal Height	6	16.1-20.3	18.6
APD	5	24.0-27.9	25.7
Proximal TD	5	14.4-18.6	16.1
Unciform			
Maximal Height	4	12.2-15.2	14.2
APD	4	20.0-24.0	22.3
Proximal TD	4	13.0-17.2	14.9
Metacarpal			
Length	7	242.0-275.0	263.0
Proximal APD	9	21.0-27.4	23.2
Proximal TD	10	29.4-38.0	32.5
Distal APD	8	21.6-26.4	24.1
Distal TD	10	32.0-39.3	35.8
Talus			
Lateral Length	9	38.5-46.3	42.3
Medial Length	9	36.2-44.0	40.7
Lateral APD	10	19.7-27.5	23.0
Medial APD	8	21.5-25.0	24.1
Distal TD	9	22.5-28.8	25.8
Calcaneum			
Length	7	94.0-106.0	100.2
c.c. Length	9	61.0-75.4	67.9
t.c. APD	8	23.1-27.7	25.9

	N	OR	M
t.c. TD	8	20.1-23.2	21.6
m. APD	6	32.0-39.5	36.2
s. TD	6	26.6-30.2	28.2
Navicular-cuboid			
Anterior Height	8	19.4-25.5	21.7
Posterior Height	5	25.1-29.0	27.2
Maximal APD	7	34.2-40.0	36.2
Maximal TD	8	31.4-36.6	33.6
Metatarsal			
Length	6	252.0-280.0	266.0
Proximal APD	18	29.0-40.0	32.1
Proximal TD	18	26.2-33.0	28.7
Distal APD	10	19.2-25.3	22.0
Distal TD	10	29.1-37.5	33.2
I Phalanx			
Length	13	46.5-57.4	51.6
Proximal APD	12	18.9-22.6	21.0
Proximal TD	13	15.1-19.3	17.3
Distal APD	14	10.5-15.0	13.3
Distal TD	15	12.5-15.8	14.5
I			
I Phalanx			
Length	8	26.5-30.5	28.4
Proximal APD	8	17.1-21.0	19.5
Proximal TD	9	13.0-16.0	14.5
Distal APD	9	14.3-17.6	16.4
Distal TD	9	10.2-14.4	12.0
III Phalanx			
Plantar Length	8	30.1-36.6	33.6
Dorsocaudal D	5	22.7-28.0	24.8
Maximal TD	9	11.7-14.8	12.9

Magnotrapezoid	AD501'95	PQAD2574	AD609'94
Anterior Height	14.8	14.6	
APD	23.8	21.8	19.3
Anterior TD	19.2	16.8	15.0
Posterior TD	18.5	15.3	16.3

Tibia	PQAD2292	PQAD1100	PQAD42
Length	360.0	350.0	317.0
Proximal APD	71.1		
Proximal TD	64.5		59.2
Distal APD	32.1	29.4	27.2
Distal TD	39.1	35.6	34.8

which is lost in some fossil giraffids such as *Palaeotragus microdon* (Koken, 1885), *Samotherium sinensis* (Schlosser, 1903), *Deccenatherium pachecoi* Crusafont-Pairo, 1952, and *Sivatherium hendeyi* Harris, 1976, but which is still present in the two extant giraffids (*Giraffa camelopardalis* Linneaus, 1758 and *Okapia johnstoni*). In the semilunar, the distal lateral facet is somewhat wider than the medial one. The magnotrapezoid, which is similar to that of *Palaeotragus primaevus* Churcher, 1970, has a concave posterior margin and begins to develop a posterior keel between the facets for the semilunar and the scaphoid. In the unciform, the semilunar facet is particularly elongated in a posterior sense, characters which it shares with other giraffids.

Tarsus (Fig. 11E-G)
The astragalus is plesiomorphic. It is similar to that of *P. primaevus* but has a weakly expressed posterior process in the medial proximal condyle. There is no strong development of the proximal lateral condyle as occurs in *Climacoceras gentryi*, and the distal trochlea has more or less symmetrical condyles. In posterior view, the navicular cuboid shows a very strong medial crest distally which diminishes to nothing at the proximal zone. It has a fossa in a very lateral position, unlike in *P. primaevus*, *Giraffa* and *Okapia*.

Metatarsal
The proximal epiphysis of the metatarsal has similar morphology to that of *Andegameryx andegaviensis* Ginsburg *et al.*, 1994, and the anterior groove is open distally.
The metacarpal, pelvis, tibia and calcaneum all have a generalized morphology similar to that of *P. primaevus*. However, the scapula of *O. hendeyi* has a less-developed supraglenoid tubercle than that of *Palaeotragus primaevus* whereas its coracoid apophysis is more reduced than it is in the latter species.

DISCUSSION
Orangemeryx shares with other climacoceratines the same morphological pattern of the dentition and the possession of complex supraorbital apophyses. In *Nyanzameryx pickfordi* Thomas, 1984, and *Orangemeryx* the frontal apophyses are ornamented at their bases with rounded protuberances which do not project far enough to form lateral points. In contrast, in *Climacoceras africanus* MacInnes, 1936, and especially in *C. gentryi* Hamilton, 1978, the points are considerably elongated, imparting a deer-like morphology to the apophyses. The morphology of the apophyses permits us to separate the various species into two groups : one comprising the two species of *Climacoceras* plus *Nyanzameryx* Thomas, 1984, the other consisting of *Orangemeryx*.

PHYLOGENETIC RELATIONS

The relationships between these two groups, now considered to be subfamilies of the family Climacoceratidae (= Climacoceridae of Hamilton, 1978), is based on the fact that they share the same morphological pattern of the dentition and the incipient elongation of the neck and the limbs. The presence of elongated cervical vertebrae, including the atlas, was already noted in *Climacoceras gentryi* by Hamilton (1978), the atlas of which is proportionally longer than it is in *Palaeotragus primaevus* and *Samotherium africanus* Churcher, 1970. Even though no atlas of *Orangemeryx hendeyi* has been found, comparison between the axes of this species and that described by Churcher (1970) for *Palaeotragus primaevus* is suggestive in this respect, and indicates to us that this new genus also possessed a long neck.
The new fossil material described here tends to confirm this relationship because *Sperrgebietomeryx*, *Orangemeryx* and *Climacoceras* (*C. gentryi*) share elongated cervical vertebrae, including the atlas, a character which indicates a notable specialization towards feeding from high food sources. In the forms of which the postcranial skeleton is known, it is possible to confirm that the extremities are clearly elongated. The cladogram (Fig. 12) summarizes the phylogenetic relationships between the described forms, considering *Andegameryx* Ginsburg *et al.*, 1994, to be the outgroup.
The family Climacoceratidae has previously been placed close to the giraffes on the basis of the presence of a bilobed lower canine in *Climaco-*
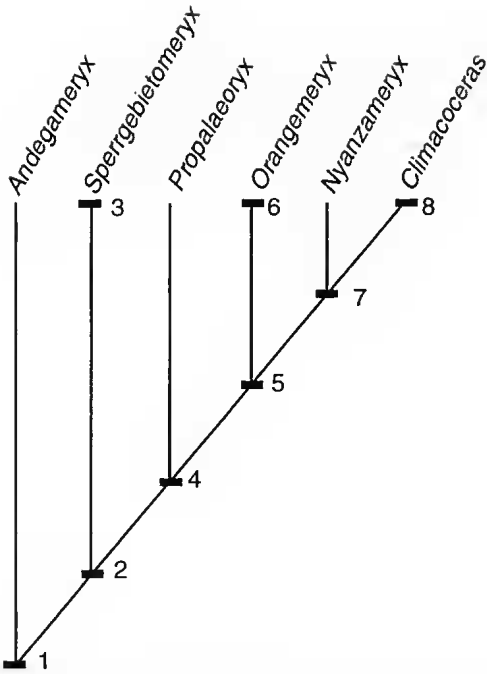
FIG. 12. — Phylogenetic relationships of *Sperrgebietomeryx* n. gen. *Propalaeoryx* Stromer and *Orangemeryx* n. gen. to other giraffoids. Nodes: 1, (primitive characters) dentition moderately hypsodont; upper and lower premolar series long; premolars elongated and thus gracile; lower molars with strong stylids; third lobe of m3 simple; hypoconid isolated, a consequence of its clear separation from the entoconid and the anterior lobe; the p4 has a simple metaconid, directed posteriorly, anterior wing simple, its morphology differing little from that of the p3; the p1 is present with two strong roots; upper premolars long. P2 and P3 with well-defined anterior lobes; upper molars with strong styles and late union of the internal lobes to the ectoloph; appendicular skeleton gracile, with a tendency to elongation of the elements; 2, cervical vertebrae, including the atlas, elongated; 3, loss of p1; 4, hypsodont dentition. The p4 with metaconid disposed more transversally, with a tendency to turn anteriorly, anterior wing bifurcate (and thus very different from p3), tendency towards flattening of the internal wall of the lower molars; 5, presence of supraorbital apophyses with protuberant ornamentations at the base, with a bifurcate termination; loss of p1, 6, apophyses with elongated slightly compressed conical morphology below the bifurcation; 7, apophyses elongated and cylindrical; 8, apophyses with well-defined points perpendicular to the long axis of the apophysis (*C. africanus*); apophyses complex, ramified as in some cervids (*C. gentryi*).

ceras gentryi from Fort Ternan (Hamilton 1978), but the presence of this character is not certain, as was noted by Churcher (1990). At Arrisdrift, there are at least sixteen lower incisiform teeth attributed to *Orangemeryx*, none of which is bilo-

bed. If fossil canines and incisors are preserved in the same ratio that occurred in life, then at least four canines should be present in the Arrisdrift sample, in which case the lower canine in *Orangemeryx* consisted of a single lobe. Other authors have advocated this relationship employing for the most part dental characters (Gentry 1994; Gentry & Hooker 1988; Janis & Scott 1987) or have merely considered it as *incertae sedis* within the Giraffoidea (Geraads 1986).

Apparently, the precocious specialisation of the postcranial skeleton separates the Climacoceratidae from the Giraffidae. Nevertheless, primitive giraffes, such as *Zarafa zelteni* Hamilton, 1973, of the early middle Miocene of Gebel Zelten, Libya, also possessed an elongated atlas. However, a deeper study of the postcranial skeleton of the forms involved in this radiation of the Giraffoidea is required before we can confirm that this specialization is a character that permits the inclusion of the Giraffidae and the Climacoceratidae in a monophyletic group.

These new ruminant fossils support the idea expressed by Ginsburg *et al.* (1994) that prior to the appearance of pecorans with frontal protuberances the group would have been strongly diversified, a diversification which affected not only the dentition, but also the postcranial skeleton. We can now determine with some precision the relationships of most of the pecoran forms lacking cranial protuberances which are related at the level of sister groups to pecoran families which do possess such protuberances. Morales *et al.* (1995) described a hornless bovid from Elisabethfeld, a discovery which corroborates this view of ruminant evolution. These findings strongly support the hypothesis that the appearance of cranial protuberances was a biological phenomenon which occurred virtually synchronously (*ca.* 18-17.5 Ma) but independently in various lineages of pecorans (comprising at least the Cervidae, Palaeomerycidae, Giraffoidea and Bovidae). It corroborates the hypothesis of Morales *et al.* (1993) in which the appearance of cranial appendages is considered to have been an organic response to global scale environmental changes which occurred towards the end of the early Miocene.

Acknowledgements

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